2. NEYMAN, J. *Lectures and conferences on mathematical statistics.* 1938. (Graduate School of the U. S. Department of Agriculture.)
3. SHEWHART, W. A. *The economic control of quality.* 1931. (Van Nostrand, New York.)
4. SMITH, D. E. *Source book in mathematics.* 1929. (McGraw-Hill, New York.)
5. WHITTAKER and ROBINSON. *Calculus of observations.* 1924. (Blackie & Son, London.)
6. FISHER, R. A. *Statistical methods for research workers.* 1932. (Oliver & Boyd, Edinburgh.)
7. SWIETOSLAWSKI, W. *Definition of absolute and comparative measurements.* Proc. 12th Conf. Int. Union Chem., Paris, p. 87. 1936.
8. WASHBURN, E. W. *The problem of establishing the identity and purity of a hydrocarbon obtained from petroleum.* Ind. Eng. Chem. **22**: 985–988. 1930.
9. SHEWHART, W. A. *Statistical methods from the viewpoint of quality control.* 1939. (Graduate School of the U. S. Department of Agriculture.)
10. ROSSINI, F. D. *Modern thermochemistry.* Chem. Reviews **18**: 233–256. 1936.
11. ROSSINI, F. D. *Heats of formation of simple organic molecules.* Ind. Eng. Chem. **29**: 1424–1430. 1937.
12. DEMING, W. E. *Least squares.* (Graduate School of the U. S. Department of Agriculture.)

PALEONTOLOGY.—*A paleoniscid brain case.*[1] THEODORE H. EATON, JR., Union College, Schenectady, N. Y. (Communicated by C. LEWIS GAZIN.)

Present sources of information on the paleoniscid neurocranium are principally three: Stensiö (1921, *Birgeria mougeoti* from the Spitzbergen Triassic), Watson (1925, *"Paleoniscid A"* and *"Paleoniscid B"* from the Kansas Carboniferous), and Case (1937, a paleoniscid similar to Watson's *"A,"* from the same horizon, Upper Pennsylvanian, Kansas City, Mo.). A specimen of the latter type, very kindly lent to me by Dr. Case, is the material for the present study. It is no. 18565, Museum of Paleontology, University of Michigan.

Important characteristics of the paleoniscid neurocranium, as shown in the papers cited, are these:

1. The brain case is tropibasic, an actinopterygian feature; that is, the large eyes have encroached on the interorbital wall until it disappeared, and the brain retreated accordingly to a position behind the eyes and between the auditory capsules.

2. Also associated with tropibasy is a myodome, a recess for the cranial attachment of the rectus eye muscles; this has eaten still farther into the brain case, beneath the anterior part of the auditory region on each side.

3. The endocranial ossifications are few but extensive, particularly a single anterior "sphenoid," paired "autosphenotics" forming the postorbital processes, and "prootico-occipitals" enclosing the auditory capsules (Stensiö, 1921). Watson (1925) found a narrow zone of chondrification separating the prootic from the occipital parts. This was confirmed by Case and is readily visible in the present specimen.

[1] Received April 27, 1939.

A distinction between the parasphenoid and basioccipital may be seen ventrally, but in general it is extremely difficult to recognize separate centers of ossification.

4. An enclosed aortic canal occurs in Watson's and Case's specimens but was not observed by Stensiö, who could give little information about the occipital region of *Birgeria*.

5. The spiracle is enclosed in a short canal.

6. Two large median fontanelles occur on the dorsal side, one anterior, the other posterior to the synotic tectum.

Stensiö made certain comparisons with other Actinopteri and with Crossopterygii; Watson carried the comparisons much farther, having better material; Case described a nearly perfect case of the brain and labyrinth, but regarding externals he simply noted a close agreement with Watson. My study adds several details of the soft anatomy, by restoration, and certain interpretations not previously made, while the publication of Romer's (1937) study of the brain case of *Megalichthys* improves greatly the possible comparisons with crossopterygians.

Specific features.—Since the genus and species can not be determined from the brain case alone, the more significant differences between brain case 18565 and that of Watson's paleoniscid A, the nearest to it, may be summarized here (see figures):

1. Aortic canal: tapers caudad in 18565, expands caudad in "A."

2. Second efferent branchial artery: shows no sign of a groove in 18565 but has a definite groove outside the foramen in "A."

3. Groove for lateral radix of dorsal aorta: runs more anteriorly than laterally in 18565, but much more laterally in "A."

4. Spiracular groove: continues far ventrad, nearly to the basipterygoid process, in 18565, but Watson shows none at all on the ventral side of "A."

5. Basipterygoid process: close against ascending process of parasphenoid in 18565, but separated from the ascending process by at least the latter's width in Watson's "A."

There are other less significant differences of proportion of parts, but these show that the specimens are at least specifically distinct. The specimen described here is remarkably good, but not perfect, and it will be impossible to discuss adequately the orbit, myodome, snout, or anterior part of the roof of the cranium. Other parts show well and with little apparent distortion. For the brain and labyrinth see Case (1937).

Spiracular region.—A ventral or dorsal view (Figs. 1, 2) shows a

large blunt projection on the side of the postorbital region. This is formed, ventrally, by the ascending process of the parasphenoid and is penetrated dorsoventrally by the spiracular canal. The jugular canal passes through more internally, in a nearly longitudinal direction, and a troughlike facet marks the position of the hyomandibular articulation, externally and behind the spiracular canal (Fig. 3). The spiracular canal opens dorsally into a fossa, which spreads caudad to a peculiar deep pit located just above the horizontal semicircular canal. This pit in the present specimen (18565) closely matches the position of the external opening of the spiracle in such a form as *Cheirolepis* (Devonian), and it may be, therefore, that the dorsal course of the spiracular duct was drawn backward. In *Amia*, which likewise has the spiracle enclosed in a canal, there is no such dorsal trough in the neurocranium, and the external opening is directly upward, behind the eye. In *Polypterus*, without an enclosed spiracular canal, there is also no such trough or more posterior pit. Yet the smooth and definite continuity of the trough in the paleoniscid makes it very difficult to imagine any other function than carrying the dorsal part of the spiracular duct.

From the ventral opening of the spiracular canal a narrow but distinct groove runs down and forward, approaching the midventral line. Clearly this carried the lower part of the spiracular duct to the roof of the pharynx.

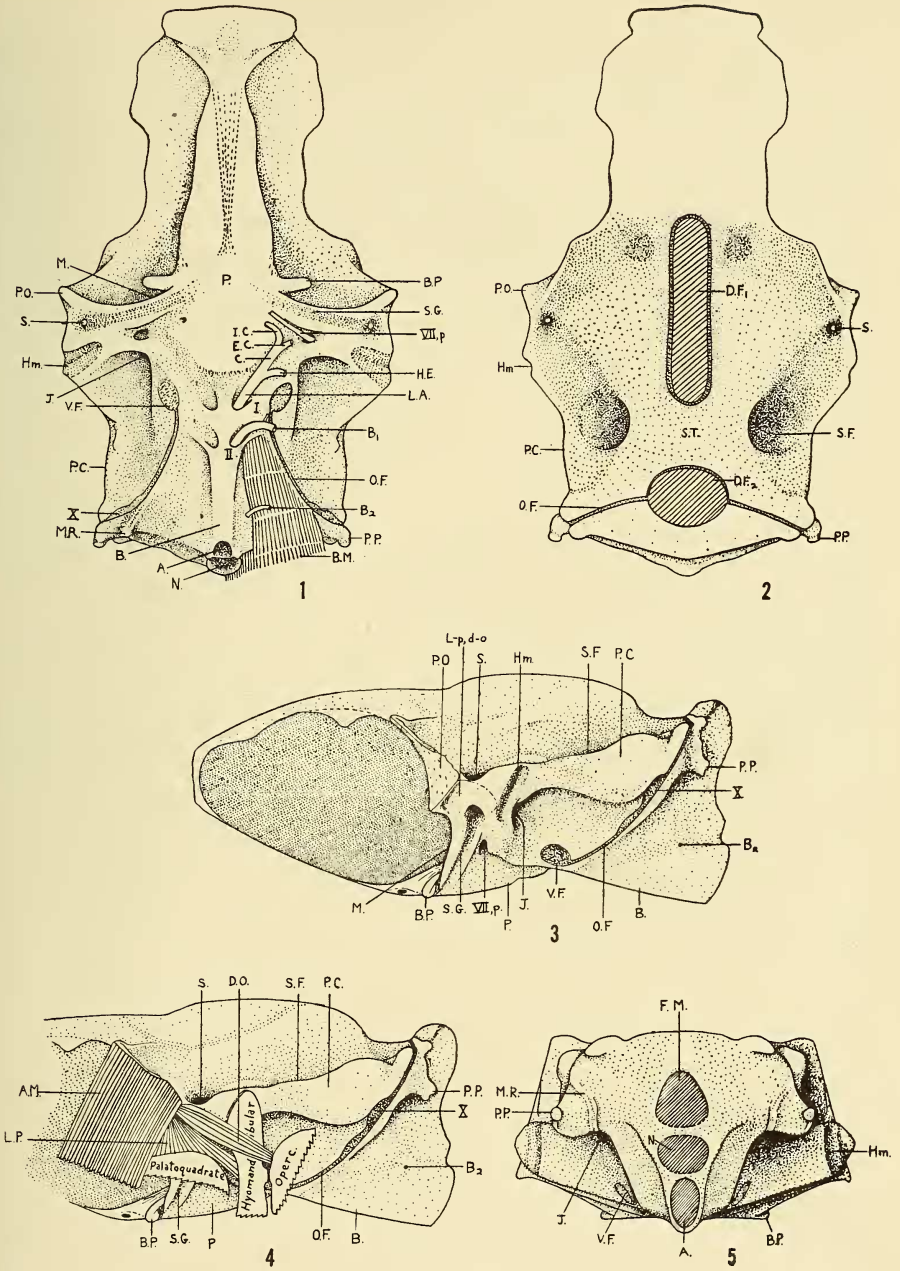
The anterior face of the postorbital process forms a triangle facing outward, and the roofing bones must have attached to it along its dorsal rim. Judging from *Amia* (Allis, 1897) and *Polypterus* (Allis, 1922) the external division of the adductor mandibulae, or a part of that division, originated on this triangular face. The internal divisions would, of course, have originated on the palatoquadrate. Then the distinct excavation behind this triangle, and lateral to the spiracular canal, housed the origin of the levator palatoquadrati and the smaller, more posterior dilator operculi. The levator palatoquadrati descends fanlike in *Amia* and *Polypterus* to insert on the dorsal edge of the palatoquadrate and anterior face of the hyomandibular. In all probability this arrangement had been established in the paleoniscids, since the amioids and Polypterini are known to represent divergent lines of descent from them. All these muscles are innervated by the trigeminus and are therefore properly jaw muscles. But the dilator operculi reaches back (in *Amia*, *Polypterus*, and other Actinopteri) across the head of the hyomandibular and inserts, usually by a tendon, on the inner face of the operculum. In most of

these fishes the distance to reach is considerable, and the muscle is nearly horizontal. In the paleoniscids, however, consideration of the parts involved suggests a fairly short muscle, and there is no evidence of a distinction, at the origin, between this and the levator palatoquadrati. (In the development of the embryo in modern Actinopteri the two arise as one, but take different insertions.) In a previous paper (Eaton, 1939) written before seeing the paleoniscid neurocranium, I suggested that the operculum of "higher" fishes, including Actinopteri, might have been derived from a mandibular type of operculum like that found in acanthodians. If so, the trigeminus innervation of the dilator operculi would be explained easily by supposing that this muscle attached to the operculum when the latter articulated with the mandibular series of bones; it would then have

---

ABBREVIATIONS FOR FIGURES

A.—Canal for dorsal aorta
A. M.—Adductor mandibulae
B.—Basioccipital
B. M.—Segmental body muscles
B_1, B_2—Branchial efferent arteries 1 and 2
B. P.—Basipterygoid process
C.—Common carotid artery
D. $F._{1,2}$—Dorsal fontanelles 1 and 2
D. O.—Dilator operculi
E. C.—External carotid artery
F. M.—Foramen magnum
H. E.—Hyoidean efferent artery
Hm.—Facet for hyomandibular
I. C.—Internal carotid artery
J.—Jugular canal
L. A.—Lateral dorsal aorta
L. P.—Levator palatoquadrati
L–p, d–o.—Origin of levator palatoquadrati and dilator operculi
M.—Location of myodome
M. R.—Ridge probably at edge of body muscles
N.—Notochord canal
O. F.—Otico-occipital fissure
P.—Parasphenoid
P. C.—Parotic crest
P. O.—Postorbital process
P. P.—Paroccipital process
S.—Spiracular canal
S. F.—Supraotic fossa
S. G.—Spiracular groove
S. T.—Synotic tectum
V. F.—Vestibular fontanelle
I, II—Probable locations of first branchial articulations
VII, p—Palatine branch of facial nerve
X—Vagus foramen



Figs. 1–5.—Paleoniscid brain case. 1, Ventral aspect, with certain details restored. Length 27 mm. 2, Dorsal aspect, anterior part incompletely preserved. 3, Lateral aspect. 4, Lateral aspect, with certain parts restored. 5, Posterior aspect. All figures about three times natural size.

followed the operculum back in a short migration to the hyomandibular after the hyoid cleft was reduced to a spiracle. The apparent shortness and obliqueness of the muscle in the paleoniscid seems to lend a new support to this idea, and might even have been predicted, since it means that the operculum was, morphologically, nearer to the jaw than in later types. This also shows externally in the apparent relations of the operculum to the dermal jaw bones.

Running back from the facet for the hyomandibular is a strong, uneven parotic crest, which extends as far as the fissure between the otic and occipital divisions of the cranium. This crest is more prominent than in any other fishes, but it is also distinct in Dipnoi (*Neoceratodus*) and Crossopterygii (*Megalichthys;* see Romer, 1937, Figs. 1, 2, 5). Watson (1925) says, "It is difficult to see any reason for the development of the lateral ridge on the otic region, which is, however, quite constant in its occurrence in Actinopterygians, and forms a very marked distinction between these fish and the Osteolepids, Dipnoi and Tetrapods." But it seems to me that the function of the ridge, and its presence in osteolepids and Dipnoi, may be made out quite clearly by considering muscle origins. In each of these groups, but not the tetrapods, several muscles originate behind the hyomandibular on the otic region, and the larger of these, the levator hyoidei and levator operculi (or opercularis) come from just such a ridge. In the Dipnoi, with the operculum and hyomandibular reduced, the muscle from this ridge is the constrictor hyoidei only, which acts in effect as the whole operculum. The parotic crest, then, forms the dorsal boundary of the gill chamber, and is continued back in the form of a paroccipital process or wing, to connect by a sheet of ligament with the supracleithrum and thus furnish also the median wall of the gill chamber. Above the ridge on the neurocranium is a recess for the origin of a part of the epaxial muscles. In Crossopterygii there is a similar ridge, but shorter, in the same place, and with a smooth lateral edge which doubtless provided for the origin of the levator hyoidei and the anterior part of the constrictor. The photograph published in *Time* (April 3, 1939) of a living coelacanth recently caught off the coast of South Africa shows a broad opercular flap extending far back, so that the constrictor (or opercularis) muscle must originate largely on the fascia of the body muscles of the neck, and only a little on the skull. This condition is much like *Neoceratodus*. Above the parotic ridge (*Megalichthys*) is a supraotic fossa, as in Dipnoi, obviously for epaxial muscles. In the paleoniscid there may have been no distinction, at their origin, between the levator hyoidei,

going to the hyomandibular, and the levator operculi (the reduced homologue of the constrictor above mentioned), but both must have been present and have originated on the lateral face of the prominent parotic crest. The shiny surface here indicates a large muscle origin. In *Polypterus* the two are scarcely distinct except at their insertions, but in *Amia* they are more so, and the levator operculi apparently forms two separate muscles. In addition, more posteriorly and ventrally in the same region, there are levator muscles for the branchial arches, but these leave no apparent marks on the paleoniscid neurocranium. The only essential difference left, then, between the parotic crest of paleoniscids and that of other fishes seems to be that there was no room for any epaxial muscles to reach forward into the supraotic fossa, mentioned before as the probable dorsal opening for the spiracular duct.

Ventral aspect.—The ventral surfaces of the parasphenoid and basioccipital together have the shape of a cross, the arms of which are the ascending processes of the parasphenoid, each marked by a shallow groove for the ventral end of the spiracular duct. Anterior to the ascending process is the orbit and the short but prominent basipterygoid process, while behind, on each side, is a deep jugular fossa. At the side of the basioccipital occurs a small oval pit, the vestibular fontanelle (Watson) from which the otico-occipital fissure runs posterodorsally (Figs. 1, 3). This fontanelle and fissure mark, evidently, the embryonic distinction between the otic region and the occipital segments added to the cranium behind it. Except during early development such a gap does not occur in the cranium of other fishes. The fissure continues up to the second fontanelle on the dorsal side, behind the synotic tectum (Fig. 2).

The dorsal aorta was enclosed in a canal within a prominent median ridge of the basioccipital (Figs. 1, 5). At the anterior end of the canal there are two pairs of foramina, the first being for the lateral radices of the aorta. A groove leads anterolaterally from each of this first pair of foramina, indicating the course of the arteries. Just in front of the vestibular fontanelle a slight smoothing of the surface suggests the location of the hyoidean efferent; anterior to this the artery would be, of course, the common carotid. A small foramen somewhat mediad from the arterial groove is for the internal carotid; the external carotid would not have entered the cranium, and its further course can not be seen. Returning to the aortic canal, the second pair of foramina would, then, have been for the first branchial efferents. Halfway between these and the posterior end of the aortic

canal a very small pair of foramina emerge from the canal, which could only have carried the second branchial efferents, but they seem disproportionally reduced. *Polypterus* is the only living actinopteran that is known to have an aortic canal enclosed in the neurocranium. It differs from the paleoniscid in that only the hyoidean and first branchial efferent arteries enter the canal, the others being behind the limits of the brain case. *Megalichthys* shows a pair of divergent aortic grooves in the base of the cranium, but they are not enclosed, and their union to form the dorsal aorta was more posterior than the end of the cranium. Otherwise, to my present knowledge, Stensiö's (1927) cephalaspid cyclostomes are the only vertebrates in which the aorta was enclosed in the neurocranium.

A distinct oval foramen at the base of each parasphenoid wing, behind the spiracular groove, and lateral to the internal carotid foramen, is evidently for the palatine branch of the seventh nerve. Watson shows a foramen on the side of the otic region, posterodorsal to the vestibular fontanelle and just below the parotic crest, for the ninth nerve, but it is not possible to see this in the present specimen. The surface there is partly disintegrated. The tenth (vagus) nerve evidently emerged from an expanded part of the otico-occipital fissure, also just below the parotic crest; the opening is double.

In *Amia* the first two branchial arches attach to the cranium at points just in front of the proximal ends of their respective efferent arteries. The first one, only, articulates with the cranium in *Polypterus*. The articulating end of the first branchial in each case is forked. The levator muscles for the arches originate laterodorsally to the gill chamber near the vagus foramen. In the paleoniscid it seems probable that the first two arches connected with the basioccipital close to the two pairs of anterior openings of the aortic canal, as indicated in Fig. 1. The location for the first one is indistinguishable, but that for the second seems to show as a faint ligament scar just behind the foramen for efferent artery 1. Presumably the levator muscles originated on the parotic crest just anterior to the vagus foramen and the otico-occipital fissure, thus being in line with the serially homologous levator hyoidei plus levator operculi.

Occipital region.—At the lateral extremity of the occiput occurs, on each side, a prominent knob projecting posteriorly, which has not been described before. This shows most clearly in the posterior view (Fig. 5). Comparison with other Actinopteri identifies it as a paroccipital process, from which a ligament extended to the post-

temporal. This comparison also clears up the interpretation of the paroccipital area in other groups of fishes. In Actinopteri, Dipnoi, and Crossopterygii the shoulder girdle is connected with the skull. In Actinopteri the connection is not only by a dermal articulation of the posttemporal with (usually) the epiotic, but also by a ligament running from a ventral process of the posttemporal to a process on the pterotic (teleosts) or opisthotic (more primitive types). The latter process is the one described here as paroccipital. The true opisthotic bone, homologous with that in tetrapods, is a cartilage bone, but apparently in the higher Actinopteri it tends to be crowded out by the dermal pterotic, sometimes erroneously called opisthotic. The process in question, with its ligament (which may ossify) remains in place regardless of which bone may form it.

In Dipnoi (*Neoceratodus*) the parotic crest previously described continues back to connect by a short broad ligament with the supracleithrum, forming the median wall of the gill chamber. In this case the end of the crest from the neurocranium is obviously the paroccipital process, functionally the same as in Actinopteri. It has the same relation to the branchial chamber and to the occipital face of the cranium, besides attaching to the shoulder girdle.

In *Megalichthys* (Romer, 1937, p. 12 and Fig. 5) there occurs a small knob whose morphological relations to the rest of the cranium are much the same as in the paleoniscid; that is, it faces posteriorly in line with the parotic crest, below the supraotic fossa and lateral to the area of greatest muscle attachment. This Romer termed provisionally the paroccipital process, remarking that it was "obviously an important point of attachment." I do not hesitate to identify it with the paroccipital process in the paleoniscid, which carried a ligament to the shoulder girdle, and I infer that it did likewise in *Megalichthys*. The process would be rather out of the way for a branchial arch articulation, as only the first one or two arches probably reached the skull and they would have been fairly near the hyomandibular facets and far more ventral than this process.

In tetrapods the arrangement of parts changes markedly on account of the loss of a shoulder girdle connection with the skull and because the loss of the operculum and the reduction of the hyomandibular eliminates the levator operculi and modifies the levator hyoidei; the latter changes its insertion to the mandible and becomes the depressor mandibulae of amphibians, reptiles, and birds. There is still a parotic crest, essentially as in fishes, above the jugular vein. Any process developed on this crest or near it would be, probably, a new

one; such, for example, as the process to which the dorsal arm of the stapes articulates in some reptiles. The term "parotic process" would perhaps be more satisfactory here. It is sometimes, but not always, used.

The area of attachment of muscles to the occipital face of the brain case seems to be as follows: from the dorsal rim down to the sides and lower corners of the foramen magnum and, ventrally, reaching forward nearly as far as the second pair of aortic canal foramina (first branchial efferent arteries); laterally the muscle area reaches to a curious low ridge near the paroccipital process. This ridge probably served for attachment of the external fascia of the epaxial muscles. The area as a whole, including the ventral extension forward, corresponds very closely with that in *Amia*. The posterior end of the parotic crest forms a knob which may have provided the most dorsolateral attachment for the muscle.

Finally, turning to the dorsal aspect of the neurocranium, it is worth noting that the two median fontanelles are practically the same as in the chondrocranium of *Acipenser*, but narrower. *Polypterus* has the anterior one divided by an "epiphysial bar," and lacks the posterior one.

SUMMARY

1. The more important ways in which the paleoniscid brain case shows relationship to that of other Actinopteri are these:

A. *General.* The skull is tropibasic and from the ventral side the parasphenoid and basioccipital appear as a cross. There is a pair of median dorsal fontanelles, one or both of which usually appear in the chondrocranium of modern Actinopteri. The muscles of the palatoquadrate, hyomandibular, and operculum appear to have been closely similar to those of *Amia* and *Polypterus*. A strong paroccipital process is present, indicating a ligament to the posttemporal as in most modern forms.

B. Resemblance to *Polypterus*. The aorta occupied a closed canal in the basioccipital; this canal, however, formed a projecting median ridge, absent in *Polypterus*. In connection with *Polypterus* De Beer (1937) shows that its lack of a myodome is evidently secondary, and is correlated with retention of the embryonic hypophysial foramen through the parasphenoid. Such a foramen is lacking in the paleoniscid, and the myodome, as with most other Actinopteri, is well developed.

C. Resemblance to *Amia*. The spiracle is enclosed in a short

canal. In general the features of the brain case are sufficiently near to those of *Amia* to make detailed comparison useful, but this seems to be the only exclusive agreement between *Amia* and the paleoniscid.

D. Resemblance to *Acipenser*. The two dorsal fontanelles of the paleoniscid are far more like those of *Acipenser* than of any others.

E. Special peculiarities. There is a deep supraotic pit connected by a trough with the spiracular canal, and the only interpretation the writer can make is that this carried the dorsal end of the spiracular duct. On the ventral side there is a groove for the spiracle, going toward the middle line. No supraotic fossa for the epaxial muscles is present. The otic and occipital portions are separated by a narrow fissure occupied by cartilage. The parotic crest, for the levator hyoidei and levator operculi, is much more conspicuous than in other Actinopteri. The ridge containing the aortic canal, in the basioccipital, projects down like a keel.

2. Points of particular interest in comparison with Dipnoi and Crossopterygii are these: The parotic crest is shown to be present in the latter two classes also, and to have the same morphological relations to the otic region, gill chamber, and the muscles of the hyomandibular and operculum. The paroccipital process of the paleoniscid is identified not only with that of the Actinopteri but with a similar process in Dipnoi and Crossopterygii, and the relations of the skull to the shoulder girdle are shown to be similar. The greatest contrast of the paleoniscid with these two classes is in its tropibasic skull, but tropibasy was achieved independently in the coelacanths.

LITERATURE CITED

Allis, E. P. *The cranial muscles and cranial and first spinal nerves in* Amia calva. Journ. Morph. **12**(3): 487–808, pls. 20–38. 1897.

——— *The cranial anatomy of* Polypterus, *with special reference to* Polypterus bichir. Journ. Anat. **56**(3, 4): 189–294, pls. 3–24. 1922.

Case, E. C. *The brain and skull of a paleoniscid fish from the Pennsylvanian of western Missouri.* Proc. Amer. Phil. Soc. **78**(1): 1–10, 2 pl. 1937.

De Beer, G. R. *Development of the vertebrate skull.* Oxford. 1937.

Eaton, T. H., Jr. *Suggestions on the evolution of the operculum of fishes.* Copeia, **1939**(1): 42–46. 1939.

Romer, A. S. *The braincase of the Carboniferous crossopterygian* Megalichthys nitidus. Bull. Mus. Comp. Zool. **82**(1): 1–73, 16 figs. 1937.

Stensiö, E. A. *Triassic fishes from Spitzbergen.* Pp. i–xxviii, 1–307, 35 pls., 90 figs. Vienna. 1921.

——— *The Downtonian and Devonian vertebrates of Spitzbergen. Part I. Cephalaspidae.* Skrifter om Svalbard og Nordishavet. Det. Norske Videnskaps-Akademi i Oslo. No. 12, 391 pp., 1 map, 103 figs., 112 pls. 1927.

Watson, D. M. S. *The structure of certain paleoniscids and the relationships of that group with other bony fishes.* Proc. Zool. Soc. London, 1925, pp. 815–870, 2 pls., 30 figs. 1925.